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Preliminary Growth Estimates of Northwestern Hawaiian Islands Spiny Lobster (*Panulirus marginatus*): Indications of Spatiotemporal Variability

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Preliminary Growth Estimates of
Northwestern Hawaiian Islands Spiny Lobster
(*Panulirus marginatus*):
Indications of Spatiotemporal Variability

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ABSTRACT

A maximum likelihood technique (GROTAG) was used to estimate growth of the commercially important Hawaiian spiny lobster, *Panulirus marginatus*, tagged at Necker Island, Northwestern Hawaiian Islands (NWHI) in 2002. The same technique was applied to data from previous tagging studies at Kure Atoll, NWHI (1979 – 1983) and French Frigate Shoals, NWHI (1981 – 1983). Results indicated that spiny lobster growth rates can vary substantially in the NWHI. For instance, the mean annual growth of 75 mm (carapace length) male lobsters ranged from 3.55 mm at Necker Island to 15.85 mm at Kure Atoll; the mean annual growth of 70 mm (carapace length) female lobster ranged from 1.86 mm at Necker Island to 15.84 mm at Kure Atoll. The coefficient of variation of growth variability estimates ranged from 0.34 to 0.69, indicating substantial individual variability. No Palinurid has shown such spatial variability, and only one species has exhibited similar variability on a temporal scale. Recognition of and accounting for the mean and individual variability in a life history trait of this important endemic species will result in more accurate stock assessments and, ultimately, further understanding of the NWHI coral reef ecosystem.

INTRODUCTION

Sustainable exploitation of commercially and recreationally valuable species requires an in-depth understanding of spatiotemporal variability in somatic growth. An important component of biomass production, growth rates also affect methods used to assess stocks including maturity schedules (Clark et al., 1999), recruitment/settlement (Wahle et al., 2004), spawner-recruit relationships (Sheehy, 2001), fishing selectivity (Jeffery and Taggart, 2000), and natural mortality (Griffiths and Harrod, 2007). Failing to account for growth variability, and its associated effects, in population models introduces biases to biomass estimates. Biased estimates can lead to inappropriate management schemes and, in extremis, stock collapse.

The commercially valuable Hawaiian spiny lobster, *Panulirus marginatus*, (Quoy and Gaimard, 1825), is endemic to the Hawaiian Archipelago and Johnston Atoll. The Hawaiian Archipelago consists of the main Hawaiian Islands (Hawaii to Niihau) and the Northwestern Hawaiian Islands (NWHI), a series of banks (e.g., islands, reefs, seamounts, and atolls) extending approximately 1900 km across the subtropical Pacific. After operating for more than 20 years and suffering a decline in catch-per-unit effort, the NWHI lobster fishery closed in 2000 because of increasing uncertainty in population models used to assess stock status. A panel of experts reviewed the models used to assess the lobster stocks and noted that they disregarded spatial heterogeneity and asynchronous dynamics among bank-specific lobster populations (Botsford et al., 2002). Punt (2003), in a study of Tasmanian rock lobster, *Jasus edwardsii*, showed that the performance of size-structured stock assessments was improved by taking into account spatial heterogeneity in growth.

To understand bank-specific population dynamics and ensure accurate stock assessments of NWHI spiny lobsters, an extensive tag/recapture program was initiated at Necker Island, NWHI in 2002. Growth rates can be determined from lobsters that were recaptured in 2002–2003. Previous NWHI spiny lobster tagging studies, conducted at Kure Atoll in 1979–1983 and French Frigate Shoals in 1981–1983 used the Fabens' (1965) method to estimate the conventional von Bertalanffy growth parameters L_{∞} (average maximum body length) and K (a constant describing how rapidly L_{∞} is achieved) (MacDonald, 1984). This method has since been criticized because it does not account for individual variability in growth and the high correlation between K and L_{∞} (Francis, 1988a). Francis (1988b) developed and recommended a maximum likelihood approach to describe growth from tagging data. Francis' (1988b) method provides growth estimates at two specific sizes that have better statistical properties than K and L_{∞} , particularly when the entire size range of the species is not represented in the data (Francis, 1988a, 1988b). Growth rates at these specific sizes are directly observable and are, therefore, biologically meaningful relative to K and L_{∞} (Francis, 1988a, 1988b; Haddon, 2001). Further, the method allows for estimation of individual growth variability. Not explicitly accounting for this variability (i.e., assuming all individuals in a population grow according to fixed parameters) can result in biased mean growth estimates (Sainsbury, 1980; Tyler and Rose, 1994).

The purpose of this study was to use Francis' (1988b) method to: (1) estimate growth rates (mean growth and individual growth variability) for spiny lobsters at Necker Island (2002–2003), and (2) reanalyze the Kure Atoll (1979–1983) and French Frigate Shoals (1981–1983) spiny lobster tagging data. In addition to providing recent spiny lobsters growth estimates, this will allow identification of any mean and individual growth variability in NWHI spiny lobsters.

METHODS

Tagging Data

Necker Island lobsters were captured using standard, commercial-style Fathoms Plus (San Diego, CA) polyethylene plastic traps. Captured lobsters were measured for carapace length (CL, to the nearest .01 mm) and tagged with polyethylene streamer tags (Hallprint, Inc., Victor Harbor, South Australia) inserted through the abdominal flexor muscle at the juncture of the cephalothorax and abdomen. Tag/recapture operations were performed on two chartered commercial fishing vessels during September and October of 2002 (83 recaptures) and 2003 (483 recaptures). Average time-at-liberty was 308 days (range 1–383 days) and length-at-recapture ranged 67.98–121.53 mm CL.

Lobster tagging operations at Kure Atoll and French Frigate Shoals are described in MacDonald (1984). Lobsters at Kure Atoll and French Frigate Shoals were tagged using the same tag type used at Necker Island. Tagging at both banks occurred from May through September, with the exception of January and December in 1979–1981 at Kure Atoll. Lobsters at Kure Atoll were tagged (785 recaptures) between 1979 and 1983. Average time-at-liberty of the recaptures used in the analysis was 461 days (range 1–1512), and length-at-recapture ranged from 60.6 to 157.7 mm CL. Lobsters at French Frigate Shoals were tagged (121 recaptures) between 1981 and 1983. Average time-at-liberty of the recaptures used in the analysis was 270 days (range 1–729 days), and length-at-recapture ranged from 49.4 to 133.5 mm CL.

Growth Analysis

Location (bank) and sex-specific data were fitted to the von Bertalanffy growth equation with Francis' (1988b) maximum likelihood method using the GROTAG program designed for the Microsoft Excel solver function (Simpfendorfer, 2000). In this method, a reparameterization of the Fabens (1965) growth model, K and L_{∞} , are replaced by two alternative parameters, g_{α} and g_{β} , which represent mean annual growth increments (mm/yr) of chosen reference lengths α and β (Francis, 1988b). Following Francis (1988b), the expected length increment, ΔL , for a lobster tagged at length L_1 at liberty for time ΔT is given by:

$$\Delta L = \left\{ \frac{\beta g_{\alpha} - \alpha g_{\beta}}{g_{\alpha} - g_{\beta}} - L_1 \right\} \left\{ 1 - \left[1 + \frac{g_{\alpha} - g_{\beta}}{\alpha - \beta} \right]^{\Delta T} \right\}$$

(1)

The model was fit using the likelihood function (Francis 1988b):

$$\lambda = \sum_i \log[(1-p)\lambda_i + p/R]$$

(2)

$$\text{where } \lambda_i = \exp \frac{-1/2(\Delta L_i - \mu_i - m)^2 / (\sigma_i^2 + s^2)}{[2\pi(\sigma_i^2 + s^2)]^{1/2}},$$

(3)

R = the range of observed growth increments, μ = the expected growth increment, and σ = the standard deviation of the growth variability. Also estimated were the coefficient of variation of growth variability (v), the mean (m) and standard deviation (s) of measurement error, and outlier contamination (p). To describe growth variability, σ was related to μ ($\sigma_i = v\mu_i$), assuming an increase in growth variability as the size of the growth increment increases (Francis, 1988b).

The first model fit was the simplest, fitted with g_α , g_β , and s . Each subsequent model introduced an additional parameter in a stepwise manner. Likelihood ratio tests were used to determine the final model; for a significant ($P < 0.05$) improvement in fit, the likelihood value must increase by at least 1.92 with the introduction of one parameter and 3.0 with the introduction of two parameters (Francis, 1988b). Ninety-five percent confidence intervals were estimated using a bootstrapping method as implemented in GROTAG (Simpendorfer, 2000).

The reference lengths, α and β , were chosen so that the majority of individuals in each data set fell between these two values (Francis, 1988b). The male Necker Island and French Frigate Shoals α and β were set at 75 mm CL and 110 mm CL, respectively, whereas α and β were set at 70 mm CL and 100 mm CL, respectively, for females. Initial attempts to fit the Kure Atoll data using these values of β resulted in a lack of fit as indicated by various residual plots (data not shown). Therefore, β was set at 145 mm CL for males and 135 mm CL for females from Kure Atoll. To directly compare lobster growth from Kure Atoll with lobster growth from the other two banks, the mean annual growth rate of all sizes (g_γ) was determined from final model outputs for each data set using (Francis, 1988b):

$$g_\gamma = ((\gamma - \alpha)g_\beta + (\beta - \gamma)g_\alpha) / (\beta - \alpha)$$

(4)

RESULTS

The model containing g_α , g_β , s , v , m resulted in the best fit to the Necker Island data and models containing g_α , g_β , s , v resulted in the best fit to both the Kure Atoll and the French Frigate Shoals data. Residual distributions (length at tagging, expected growth, time at liberty) for all data sets showed no patterns indicating satisfactory fits, and the GROTAG model is appropriate for the NWHI lobster tagging data.

Male spiny lobster estimates of g_α and g_{110} (g_β for Necker Island and French Frigate Shoals; as estimated using formula 4 for Kure Atoll males (8.46 mm)) indicated growth was greatest at Kure Atoll in 1979–1983, followed by French Frigate Shoals in 1981–1983, and Necker Island in 2002–2003 (Table 1, Fig. 1). Females lobsters exhibited the same pattern as indicated by estimates of g_α and g_{100} (g_β for Necker Island and French Frigate Shoals; as estimated using formula 4 for Kure Atoll females (8.72 mm)) (Table 1, Fig. 1). Growth rates of 75 mm CL and 110 mm CL male lobsters at Necker Island were, on average, one-fourth that of those at Kure Atoll and French Frigate Shoals. Differences were more pronounced for female lobsters, with Necker Island growth rates being, on average, one-seventh at 70 mm CL and one-tenth at 100 mm CL than those at Kure Atoll and French Frigate Shoals. There were smaller differences in growth between Kure Atoll male and female lobsters and those at French Frigate Shoals. The estimated coefficient of variation of growth variability (v) for all data sets ranged from 0.34 to 0.69 indicating substantial individual variability in growth within each data set (Table 1).

GROTAG results and confidence intervals are shown in Table 1. To test estimates of m and s , independent values were estimated based on differences in length-at-tagging and length-at-recapture for individuals recaptured within 2 days of tagging at Necker Island ($n = 74$). The mean and standard deviation of these differences represents an exact measure of measurement error, assuming no growth occurred between tagging and recapture. It is likely that researchers would detect a lobster that molted within this time period (clean carapace, soft shell). The estimated mean and standard deviation of the differences in size was 0.17 mm and 0.13 mm, respectively for males and 0.22 mm and 0.22 mm, respectively for females. The Francis (1988b) method produced similar estimates of m and s (Table 1).

DISCUSSION

The Francis (1988b) method has been successfully used to estimate growth of lobsters (McGarvey et al., 1999), sharks (Simpfendorfer, 2000), teleosts (Francis et al., 1999; Welsford and Lyle, 2005) and clams (Cranfield and Michael, 2001). The same method generated NWHI spiny lobster growth estimates that show considerable differences in growth between lobsters from Necker Island (2002–2003) and both Kure Atoll (1979–1983) and French Frigate Shoals (1981–1983). Smaller differences in growth rates were also detected between lobsters from Kure Atoll (1979–1983) and French Frigate Shoals (1981–1983).

Estimated growth variability (v) values indicated substantial individual variability in growth of size classes within each data set.

Direct comparison of spiny lobster growth rates among the Necker Island, Kure Atoll, and French Frigate Shoals data sets are problematic because the capture methods differ and the data are spatially and temporally confounded. Despite these complications, the estimated growth parameters indicate that NWHI spiny lobsters can exhibit large variability in growth rates. Some natural spatiotemporal variability in lobster growth would be expected because of the spatial extent of the NWHI; decapod crustacean growth is controlled by factors that vary within a species range such as density dependency (Pollock, 1991), temperature (Chittleborough, 1975), and food availability (Newman and Pollock, 1974).

The magnitude of the differences in growth rates reported here, however, was unexpected. Although other Palinurids have shown spatial differences in growth rates (Pollock, 1991; McGarvey et al., 1999), the growth differences between the areas with the slowest growing individuals and the areas with the fastest growing individuals were not of the same magnitude as NWHI spiny lobsters. Temporal differences in growth, similar to NWHI lobsters, were exhibited in South African *Jasus lalandii* (Pollock et al., 1997). These differences are thought to be caused by a prolonged El Niño-Southern Oscillation event (Pollock et al., 1997).

The factors driving NWHI spiny lobster growth variability are currently unknown. Ongoing research includes the expansion of tagging to other banks (Gardner Pinnacles, Maro Reef, and Laysan Island) to examine the spatial and temporal (2002–2008) extent of the growth variability. Polovina (1989) documented density dependence in growth of NWHI *P. marginatus* by exploring the relationship of density, asymptotic length, and the ratio of natural mortality to growth before and after the maturation of the commercial fishery. Another possible explanation of the growth variability is oceanographic conditions. Variation in ocean productivity, as indicated by sea surface height measurements and the location of the North Pacific Transition Zone Chlorophyll Front, has significantly impacted several trophic levels in the NWHI (Polovina et al., 1994; Baker et al., 2007) and, therefore, it is probable that spiny lobster growth could also be affected. Regressing growth rates estimated from the tagging data vs. catch rates from the tagging research cruises and indicators of climate variability (temperature, sea-level) will allow insights into the causes of the observed growth variability.

The results from this tagging study indicated that spiny lobsters are capable of exhibiting substantial variability in mean and individual growth rates, both between banks and within a bank. Such variability should be taken into account in stock assessments of NWHI lobsters, along with other aspects of spatial heterogeneity and asynchronous dynamics. In an ecosystem context, recognition of variability in a life history trait of this important endemic species ultimately will further understanding of the NWHI coral reef ecosystem.

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Table 1.--Final model set values (α , β) and the estimated growth parameters (95% confidence intervals) using the Francis (1988b) method for NWHI *Panulirus marginatus*. KA = Kure Atoll, FFS = French Frigate Shoals, NI = Necker Island.

Bank, sex	α (mm)	B (mm)	g_{α} (mm/yr)	g_{β} (mm/yr)	v (mm/yr)	s (mm)	m (mm)	n
KA, male	75	145	15.85 (15.14-16.51)	1.06 (0.81-1.30)	0.51 (0.46-0.56)	0.95 (0.70-1.17)	—	439
KA, female	70	135	15.84 (15.20-16.41)	0.41 (0.06-0.78)	0.44 (0.40-0.49)	0.99 (0.74-1.21)	—	345
FFS, male	75	110	11.84 (10.75-13.04)	5.01 (4.52-5.49)	0.34 (0.25-0.42)	0.76 (0.40-1.07)	—	80
FFS, female	70	100	10.99 (9.34-13.12)	7.04 (5.05-9.01)	0.56 (0.39-0.70)	0.05 (0.02-0.08)	—	41
NI, male	75	110	3.55 (3.18-3.90)	1.65 (1.36-1.92)	0.58 (0.50-0.65)	0.19 (0.14-0.23)	0.16 (0.09-0.23)	253
NI, female	70	100	1.86 (1.56-2.05)	0.51 (0.29-0.62)	0.69 (0.57-0.80)	0.26 (0.23-0.56)	0.22 (0.15-0.34)	313

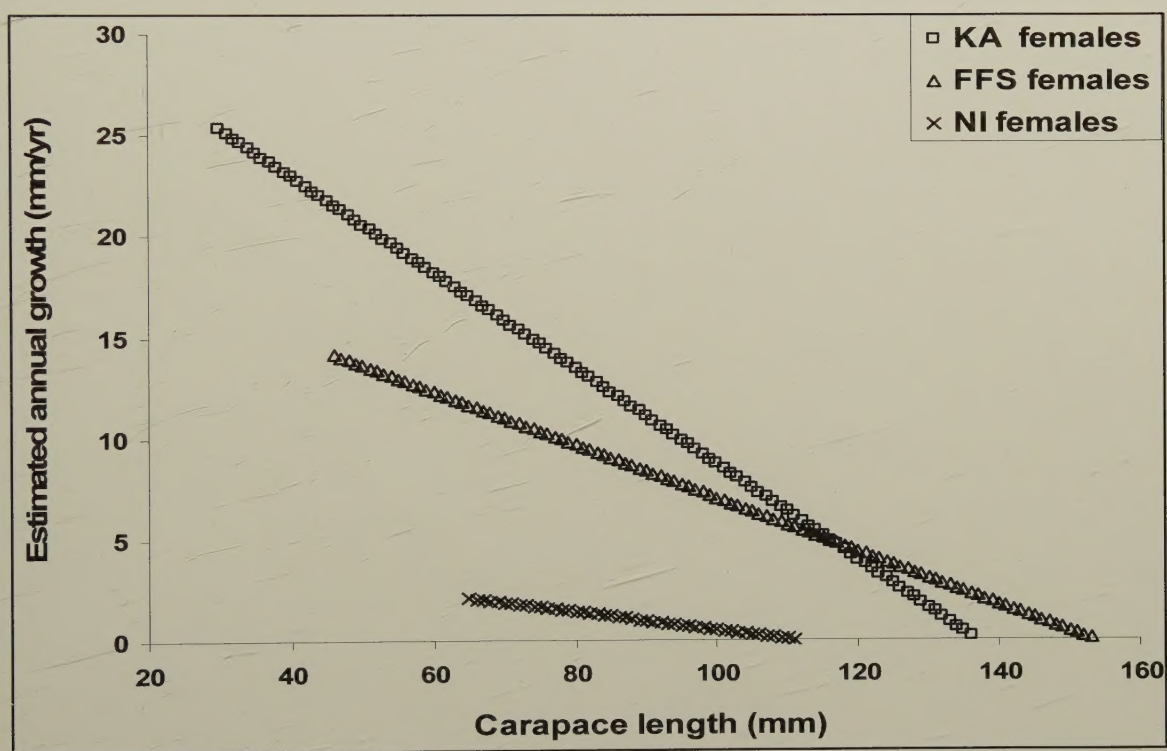
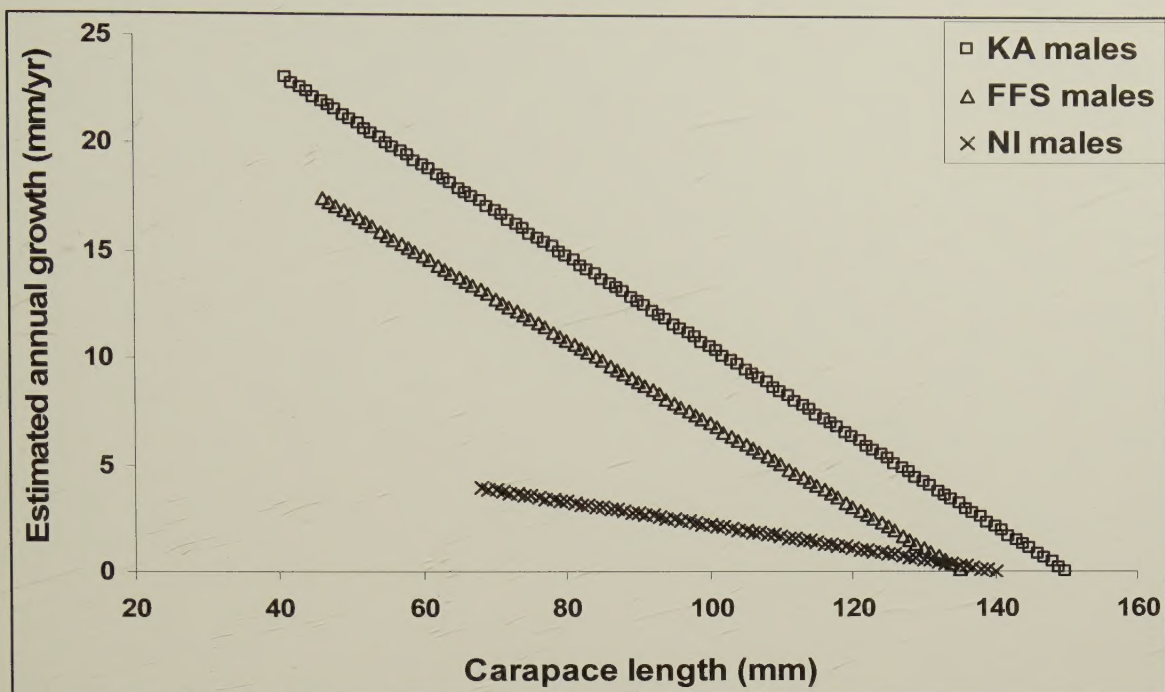


Figure 1.--Estimated growth rates of male (top panel) and female (bottom panel) *P. marginatus*. KA = lobsters tagged at Kure Atoll (1979–1983), FFS = lobsters tagged at French Frigate Shoals (1981–1983), NI = lobsters tagged at Necker Island (2002–2003).

